Phylogenetic analysis of the subfamily Colinae (Neogastropoda: Buccinidae) based on morphological characters

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ABSTRACT

Colinae Gray, 1857, the most abundant and diverse subfamily of whelks in the northwestern Pacific and Far-Eastern Seas of Russia, includes several conchologically similar genera or subgenera of unclear status and composition. Based on morphological and anatomical studies of 38 species attributed to the genera *Colus* Röding, 1799, *Plicifusus* Dall, 1902, *Latisipho* Dall, 1916, *Aulacofusus* Dall, 1918, *Retifusus* Dall, 1916, *Retimohnia* McLean, 1995, and *Pararetifusus* Kosuge, 1967, a partial generic revision and phylogenetic analysis based on 34 characters is produced. The resulting majority rule consensus tree well resolves the genera *Plicifusus*, *Retifusus*, *Pararetifusus*, and *Aulacofusus*. The genus *Retimohnia* appears to be a junior synonym of the genus *Retifusus*. Species of the heterogeneous genus *Colus* included in this study do not form a clade, indicating that this genus, as presently understood, is paraphyletic. Our results demonstrate the importance and utility of anatomical characters for resolving the systematics of the extremely diverse and variable family Buccinidae.

Additional keywords: Taxonomy, phylogeny, cladistics, northwestern Pacific

INTRODUCTION

Although the number of papers dedicated to the molecular phylogeny of neogastropods continues to increase, there is no parallel increase in data on their morphology and anatomy. This is especially true for the Buccinidae, a large and evolutionarily successful family of predatory marine gastropods that are widespread in polar, temperate, and tropical waters of the World Ocean, and which have significant commercial value. In the northwestern Pacific, Buccinidae is one of the dominant families, and in waters of the Russian Far-East, it is the most abundant and diverse family, comprising more than 30% of the total number of gastropod species (Kantor and Sysoev, 2006). Six buccinid subfamilies are present in the northwestern Pacific: Buccininae Rafinesque, 1815; Colinae Gray, 1857; Beringiinae Golikov and Starobogatov, 1975; Aneistrolepidinae Habe and Sato, 1973; Parancistrolepidinae Habe, 1972; and Volutopsiinae Habe and Sato, 1973. The subfamily Colinae (previously better known under the name Neptuneinae Stimpson, 1865) is the most diverse with respect to the number of genera and species in the northwestern Pacific (Kantor and Sysoev, 2005, 2006). It includes 16 of the 34 genera and 116 of the 263 species of Buccinidae recorded in the fauna of Russia.

The best known representative of this subfamily is the diverse genus *Neptunea*, which has had two recent revisions (Golikov, 1963; Fraussen and Terryn, 2007). Other genera, with species that do not grow to commercial size, have not attracted sufficient attention of malacologists. Among them are several conchologically similar genera with unclear taxonomic status and species composition, including: *Colus* Röding, 1799, *Latisipho* Dall, 1916, *Plicifusus* Dall, 1902, *Aulacofusus* Dall, 1918, *Retifusus* Dall, 1916, *Pararetifusus* Kosuge, 1967, and *Retimohnia* McLean, 1995.

Species and genera within Buccinidae have generally been diagnosed based primarily on conchological characters, with radular morphology contributing only occasionally to their taxonomy. Anatomical characters have, thus far, hardly been used for these purposes.

The aim of this publication is to clarify the status and composition of the genera *Colus* Röding, 1799, *Plicifusus* Dall, 1902, *Latisipho* Dall, 1916, *Aulacofusus* Dall, 1918, *Retifusus* Dall, 1916, *Retimohnia* McLean, 1995, and *Pararetifusus* Kosuge, 1967, based on conchological, anatomical and radular characters, as well as to evaluate the utility of morphological characters for resolving the taxonomy of Colinae.

MATERIALS AND METHODS

We dissected and analyzed the anatomy of 38 species of Colinae, defining 34 characters coded as 82 character states that were used to perform the phylogenetic analyses of these taxa (Table 1, Appendix 1). Of these, 7 characters described shell structure, 5 characters the

soft body and the mantle, 5 characters the reproductive systems, 12 characters the digestive system, and 5 characters the structure of the radula. The material for the study was obtained from the Zoological Institute (Saint Petersburg, Russia), the P. P. Shirshov Institute of Oceanology of Russian Academy of Sciences (Moscow), and the Zoological Museum of Moscow State University. In total, nearly 200 specimens were dissected. While processing this material, standard zoological methods were used, such as manual dissection, histology and scanning electron microscopy for the examination of radulae. Phylogenetic analyses were run using Paup*4 (Swofford, 1998).

RESULTS

Brief Descriptions of the Taxonomically Informative Morphological Characters of the Studied Genera: The gross anatomy of Colinae is typical of the Buccinidae in general features (Figures 1–2). The operculum may have a terminal (*Latisipho, Colus, Aulacofusus*; Figures 1, 26), or subspiral nucleus (*Pararetifusus*; Figure 4). The mantle cavity spans approximately one whorl of the body (Figure 3). The ctenidium (**ct**), osphradium (**os**) and, in females, the capsule gland (**cg**) can be observed by partial transparency of the mantle. Relative sizes of the ctenidium and osphradium vary in different species.

Penis morphology was used successfully by Golikov (1963, 1980) for taxonomic studies of the genera *Neptunea* and *Buccinum*; however, in our study, the structure of the distal section of penis varied very little. In *Latisipho, Plicifusus,* two species of *Colus*, and several *Retifusus* species, the seminal duct opens at the tip of a large, cone-shaped papilla (Figures 6, 8–9, **sp**) that is encircled by a fold of skin (**cf**). In the remaining *Retifusus* species, the seminal papilla is very small and becomes narrower towards its tip (Figure 10, **sp**). In the genus *Pararetifusus*, the seminal papilla is absent, with the male orifice situated terminally at the tapering tip of the penis (Figure 5). The structure of the pallial gonoduct in females appeared to be even more conservative in the genera studied. In the majority of species we examined, the vagina is strongly developed (Figure 11), occupying a ventral position on the capsule gland. Only in the genus *Pararetifusus* it is situated terminally.

The mouth opening is situated at the tip of a more or less elongated proboscis (Figure 12, **mo**). While contracted, the proboscis is situated within the rhynchodeum (Figure 12, **rd**). The anterior section of the rhynchodeum is immovable and attached to the body haemocoel walls by multiple tensor muscles. The posterior section of the rhynchodeum is capable of being everted. The proboscis is retracted by retractor muscles attached to the rhynchodeum walls (Figure 12–15, **prr**). The longest proboscises in the contracted state were found in *Aulacofusus* and in some species of *Colus*, where they are folded within the rhynchodeum (Figure 14). In other genera (*Plicifusus, Retifusus,* and *Latisipho*), the proboscis remains straight within the rhynchodeum (Figures 12–13), and elongates mostly due to eversion of the posterior, movable section.

The proboscis wall is formed of an epithelium, one or two layers of circular muscle fibers, and two layers of longitudinal muscle fibers. The sequence of layers in the majority of studied genera (*Aulacofusus*, *Latisipho*, *Retifusus*) is, (from outer to inner surfaces): epithelium, circular muscle layer, longitudinal muscle layer, circular muscle layer, and an innermost longitudinal muscle layer (Figures 18–20). In two studied species of *Plicifusus*, the sequence of layers differed, consisting of: epithelium, longitudinal muscle layer, circular muscle layer, and longitudinal muscle layer in *P. hastarius* (Figure 24), with the addition of an innermost, second layer of circular muscle fibers in *P. rhyssus*.

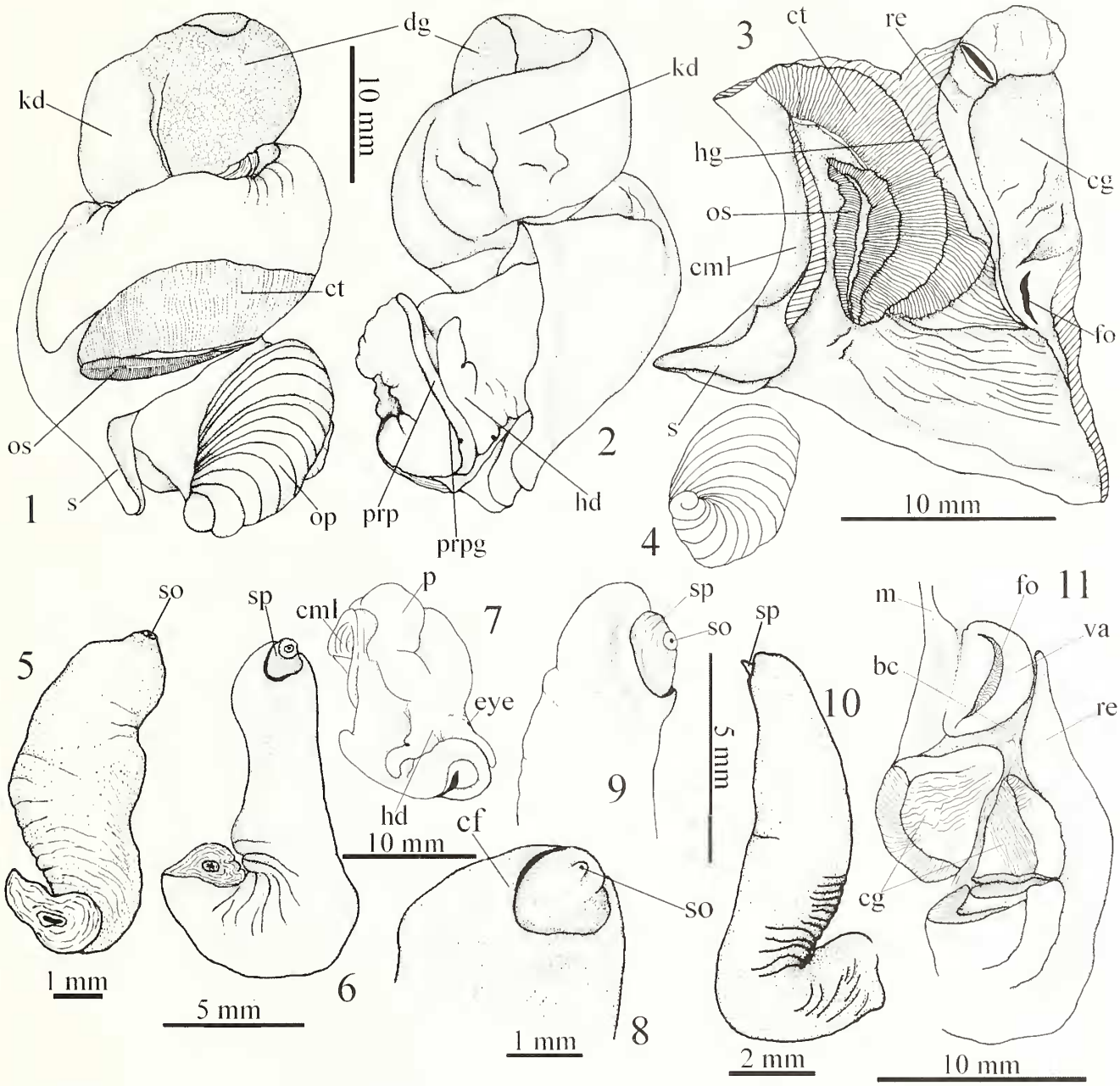
Within the proboscis is the buccal mass with radula. Comparative lengths of the buccal mass varied among taxa and have taxonomic significance. Each row of the radula (Figures 36–41) consists of two lateral teeth and one central tooth, each normally bearing 3 cusps. Although the teeth are similar in shape, the finer details are specific for genera (see below in the discussion).

The anterior esophagus opens into a large (*Retifusus, Pararetifusus*) or medium-sized (*Latisipho, Plicifusus, Colus, Aulacofusus*) valve of Leiblein (Figure 12, **vl**). The gland of Leiblein is present in all studied species (Figures 12–13, **gl**). Salivary glands differ in shape and in size (Figures 12–14, **sg**), being largest in *Retifusus* and *Aulacofusus*. The salivary ducts leave the inner side of each gland and run along the esophagus to their openings into the posterior part of the buccal cavity. The diameter and the structure of the wall of the ducts vary among different genera. In *Latisipho*, *Plicifusus*, and *Colus*, the ducts are thin and coiled (Figure 13, **sd**), while in *Aulacofusus*, *Retifusus*, and *Pararetifusus*, they are thick, sometimes with swellings in a form of a sac (salivary sacs) (Figure 15, **ss**). In *Aulacofusus*, the walls of salivary ducts have an additional layer of longitudinal nucles (Figure 21, **lm**). The posterior esophagus opens into the stomach. The structure of the stomach is generally of the same type in the majority of the species studied, but the length of the posterior mixing area can differ among genera (Figure 16–17, **pma**).

Phylogenetic Analyses: *Volutopsius norvegicus* (Gmelin, 1791) (Buccinidae: Volutopsiinae) and *Ancistrolepis okhotensis* Dall, 1925 (Buccinidae: Ancistrolepidinae), whose anatomy is known (Kantor, 1982, 1988), were used as outgroups. A heuristic search yielded 2624 trees, each 147 steps in length. Consistency index (CI) = 0.3197, homoplasy index (HI) = 0.6803, retention index (RI) = 0.6942. Figure 25 shows the 50% majority-rule consensus tree.

Several clades can be distinguished within the ingroup (Clades 1 to 6, Figure 25).

Clade 1, which is supported in 93 percent of trees, corresponds to the genus *Plicifusus*, and contains 12 species, including the type species of *Plicifusus*. At the moment, we prefer to treat it as a monophyletic genus pending examinations of additional species.



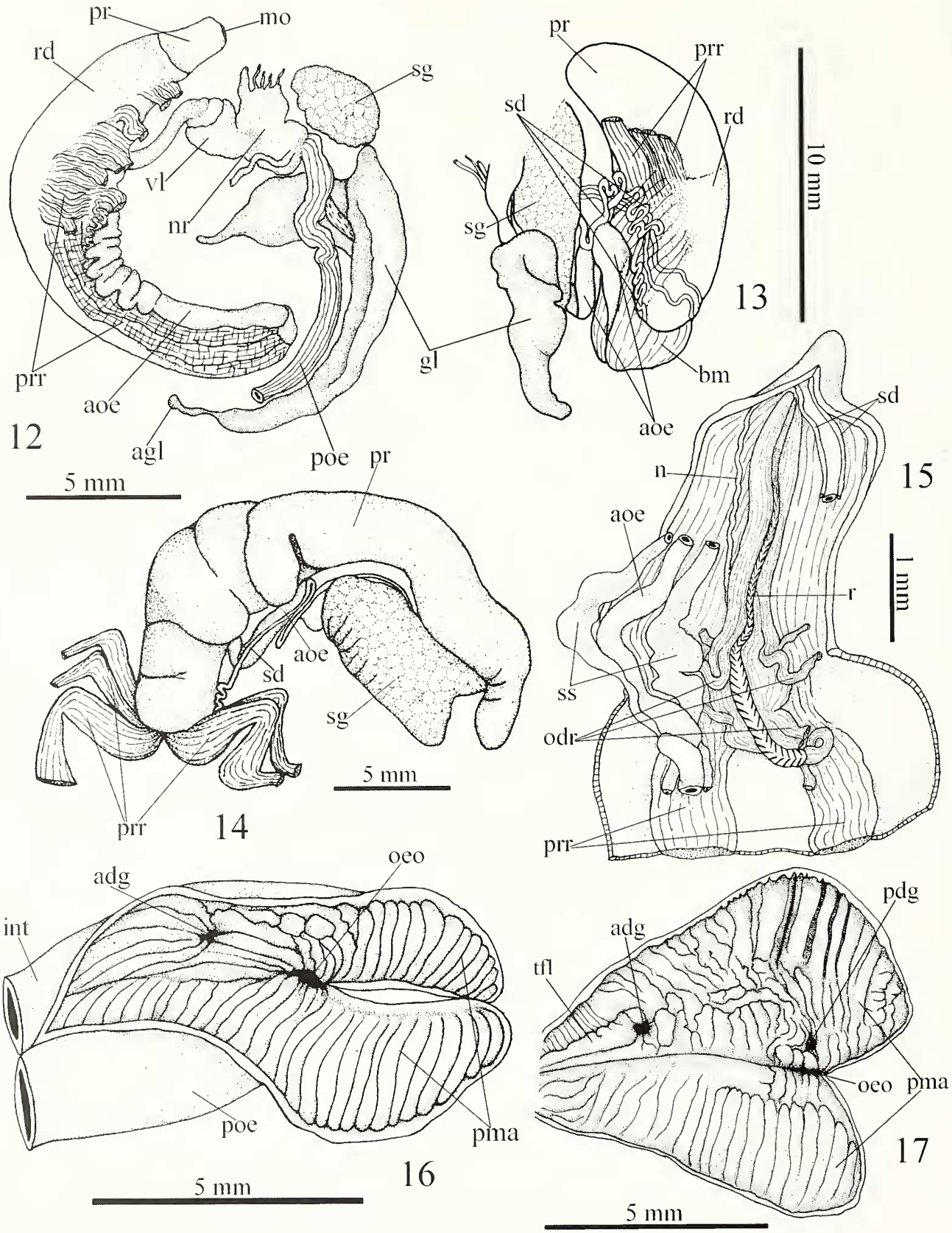
Figures 1–11. Anatomy. **1–2.** *Plicifusus bambusus*. **3.** Mantle of *Plicifusus hastarius*. **4.** Operculum of *Pararetifusus kantori*. 5. Penis of *Pararetifusus kantori*. **6, 8.** Penis of *Latisipho hallii*, ventral view. **7.** Frontal-dorsal view of the soft body of *Colus minor*, with mantle removed. **9.** Upper section of penis of *Colus minor*. **10.** Penis of *Rctifusus jessoensis*. **11.** Pallial female reproductive system of *Plicifusus rhyssus*, capsule gland, opened dorsally. Abbreviations: **bc,** bursa copulatrix; **cf,** circular fold of skin around the seminal papilla; **cg,** capsule gland; **cml,** columellar muscle; **ct,** ctenidium; **dg,** digestive gland; **eye,** eye; **fo,** female orifice; **hd,** head; **hg,** hypobranchial gland; **kd,** kidney; **m,** mantle edge; **op,** operculum; **os,** osphradium; **p,** penis; **prp,** propodium; **prpg,** propodial groove; **re,** rectum; **s,** siphon; **so,** male orifice; **sp,** seminal papilla; **va,** vagina

Plicifusus Dall, 1902

Tritonofusus (Plicifusus) Dall, 1902: 523.

Type Species: *Fusus kroyeri* Möller, 1842, by original designation.

Diagnosis: The genus is characterized by an elongated, small to medium-sized fusiform shell with well-developed axial ribs and numerous spiral cords (from 30 to 60 cords on penultimate whorl) that cover the entire shell surface (Figures 31, 33). The central tooth of the radula is large and broad, and has two to four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(usually three) sharp cusps (Figure 36). The lateral teeth usually have three or four cusps, with the central cusps always smaller than the lateral ones. The salivary ducts are very thin and convoluted. The stomach is large, as compared to the proboscis, and narrow, with a small posterior mixing area.

Remarks: *Plicifusus* was described by Dall (1902) as subgenus of *Tritonofusus* Mörch, 1857, which is an objective synonym of *Colus* Röding, 1799, since it is based on the same type species. *Plicifusus* has been treated as a distinct genus by the majority of subsequent authors.

Genus Composition: The majority of the included species were described within this genus [or attributed to the subgenus *Tritonofusus (Plicifusus)*]. *Quasisipho torquatus* Petrov, 1982, is the type species of the monotypic genus *Quasisipho* Petrov, 1982, from the upper Pliocene-lower Pleistocene of eastern Kamchatka. This species survives in the Recent fauna, and its anatomy confirms that the type species belongs within *Plicifusus*. Thus *Quasisipho* becomes junior subjective synonym of *Plicifusus*. Some species were originally described or attributed to *Retifusus* [e.g., *Plicifusus (Retifusus) scissuratus* Dall, 1918]. *Tritonofusus (Plicifusus) rhyssus* Dall, 1907 was placed in the genus *Helicofusus* Dall, 1916 (type species by original designation *Tritonofusus (Plicifusus) aurantius var. latieordatus* Dall, 1907) by many Russian authors (e.g., Kantor and Sysoev, 2005, 2006).

The results of our study place the following species within the genus *Plicifusus*:

Plicifusus kroeyeri (Møller, 1842) [= *Fusus arcticus* Philippi, 1850]
Plicifusus plicatus (A. Adams, 1863)
Plicifusus scissuratus (Dall, 1918)
Plicifusus croceus (Dall, 1907)
Plicifusus elaeodes (Dall, 1907)
Plicifusus rhyssus (Dall, 1907) [= *Plicifusus (Latifusus) wakasanus* Dall, 1918; *Tritonofusus (Plicifusus) aurantius* Dall, 1907; *Plicifusus (Aulaeofusus) rhyssoides* Dall, 1918]
Plicifusus hastarius Tiba, 1980
Plicifusus bambusus Tiba, 1980
Plicifusus obtusatus Golikov *in* Golikov and Scarlato, 1985
Plicifusus olivaceus (Aurivillius, 1885) [= *Plicifusus (Retifusus) ineisus* Dall, 1919]
Plicifusus oceanodromae (Dall, 1919)
Plicifusus torquatus (Petrov, 1982)

A second, well defined clade with 100% bootstrap support includes 20 species in our study, and is composed of several well supported subclades (clades 2, 3, 4, 5) and two unresolved species.

Clade 2, although not supported in all trees, contains three northern Atlantic species of the genus *Colus* Röding, 1798 (Figure 26), including *C. islandicus*, the type species. The other two species, often attributed to *Colus: C. minor* (Dall, 1925) and *C. kujianus* Tiba, 1973, do not emerge as members of this clade. These results reflect the high heterogeneity of *Colus*, which is widely distributed in the Atlantic and Arctic Oceans and in the northern Pacific. Many more species need to be studied in detail before the taxonomy of *Colus* is clearly understood.

Clade 3 includes three species belonging to the genus *Pararetifusus*, including its type species.

Pararetifusus Kosuge, 1967

Retifusus (Pararetifusus) Kosuge, 1967: 62.

Type Species: *"Phymorhynchus?" tenuis* Okutani, 1966 (by original designation).

Diagnosis: The genus is characterized by a small shell with a relatively high last whorl. The spiral sculpture consists of a few elevated, sharp or rounded ribs; axial folds are absent (Figures 28, 30). The radula is similar to that of *Retifusus roseus, R. latieingulatus, R. similis, R. iturupus*, and *R. attenuatus* (Figure 38) (see below for description).

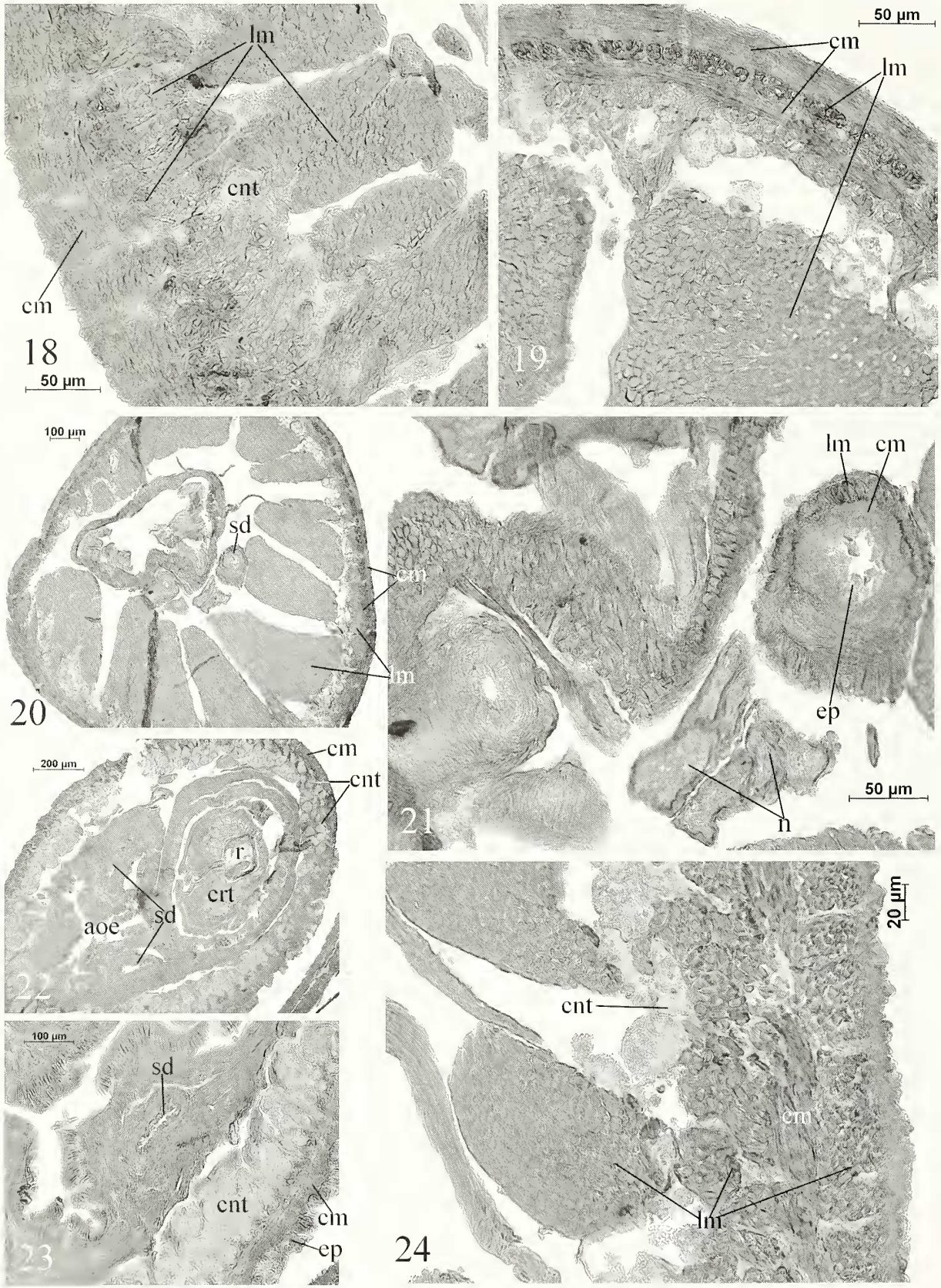
Remarks: The type species was originally placed in *Phymorhynchus* (Conoidea), but examination of the radular and morphological characters undoubtedly placed it within Buccinidae (Kosuge, 1967).

Genus Composition: Very few species have been placed in *Pararetifusus*. In addition to the species studied here (below) only one, *P. dedonderi* Fraussen and Hadorn, 2001, from Philippines was tentatively attributed to *Pararetifusus* but later excluded by Kosyan (2006a).

Pararetifusus tenuis (Okutani, 1966)
Pararetifusus kantori Kosyan, 2006
Pararetifusus kosugei Kosyan, 2006

The genus was proposed as a subgenus of *Retifusus* and is close to it in radular structure and anatomy, but differs in shell sculpture. The spiral cords of *Pararetifusus* shells are very similar to the cords of *Aulaeofusus*

Figures 12–17. Anatomy. **12.** Right lateral view of the foregut of *Plicifusus hastarius*. **13.** Left lateral view of the foregut of *Plicifusus rhyssus*. **14.** Right lateral view of the foregut of *Aulacofusus herendeeni*. **15.** Dorsally opened proboscis of *Retifusus roseus*. **16.** Opened stomach of *Aulacofusus periscelidus*. **17.** Opened stomach of *Plicifusus hastarius*. Abbreviations: **adg,** opening of anterior duct of digestive gland; **agl,** ampulla of gland of Leiblein; **aoc,** anterior esophagus; **bm,** buccal mass; **gl,** gland of Leiblein; **int,** intestine; **mo,** mouth opening; **n,** nerves; **nr,** nerve ring; **odr,** odontophore retractors; **oco,** oesophageal opening; **pdg,** opening of posterior duct of digestive gland; **pma,** posterior mixing area; **poc,** posterior esophagus; **pr,** proboscis; **prr,** proboscis retractors; **r,** radula; **rd,** rhynchodeum; **sd,** salivary duct; **sg,** salivary gland; **tfl,** typhlosole; **vl,** valve of Leiblein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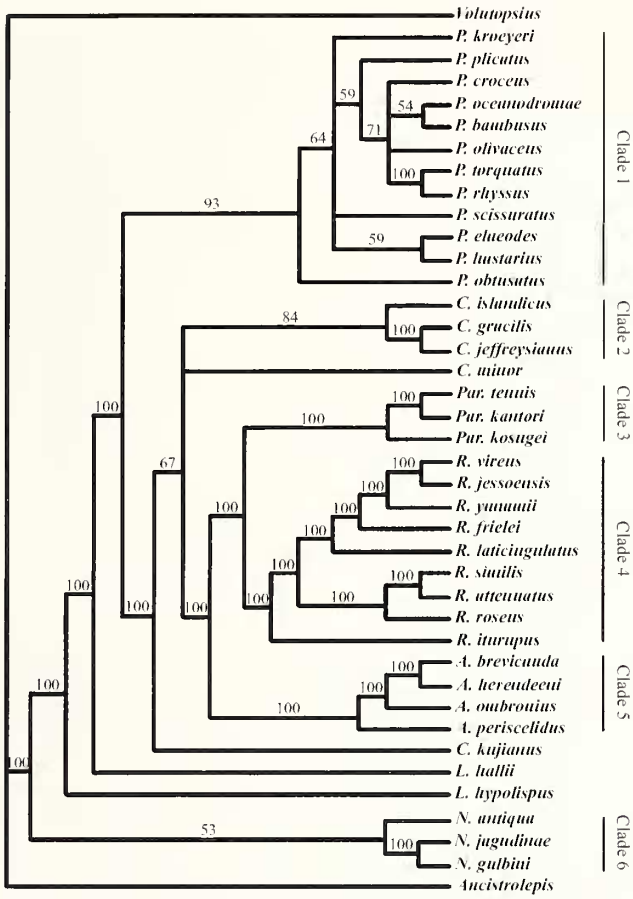


Figure 25. Fifty-percent majority-rule consensus tree obtained from 2624 trees, each 147 steps in length.

periscelidus; however, the anatomy of *Pararetifusus* differs considerably.

Clade 4, which is conchologically most heterogenous, contains 9 species previously classified within the genera *Retifusus*, *Molnia*, *Retimolnia*, and *Plicifusus*. The oldest valid name for this group is *Retifusus*.

Retifusus Dall, 1916

Plicifusus (Retifusus) Dall, 1916: 8.

Type Species: *Tritonium (Fusus) jessoensis* Schrenek, 1863 (by original designation).

Diagnosis: The genus is characterized by a small (on average < 2.5 cm) shell, which has an axial and spiral sculpture similar to that of *Plicifusus* (Figures 32, 34); however, the radula has a different morphology (Figure 37, 38). The lateral teeth usually have three or four long cusps of nearly equal length. The central teeth may be of two types. *R. jessoensis*, *R. virens*, *R. yamamii*, and *R. frielei* have five or six sharp cusps increasing in length from the periphery to the center (Figure 37). The central teeth of *R. roseus*, *R. laticingulatus*, *R. similis*, *R. iturupus*, and *R. attenuatus* have only three sharp cusps, and the central cusp is usually longer than the lateral cusps (Figure 38). The salivary ducts are very thick and straight. The stomach is large compared to the proboscis, narrow, and has a small posterior mixing area.

Remarks: McLean (1995) established the genus *Retimolnia* (type species by original designation, *Molnia frielei* (Dall, 1891) to incorporate several species previously assigned to the genus *Molnia* Friele, 1878. Our analysis demonstrates that *M. frielei* belongs to the same clade and is morphologically rather similar to *R. jessoensis*, the type species of *Retifusus*. Thus, *Retimolnia* is a junior subjective synonym of *Retifusus*. *Retifusus* is often considered to be a subgenus of *Plicifusus* (e.g., Higo et al., 1999) but our analysis demonstrates that it is not closely related to the latter.

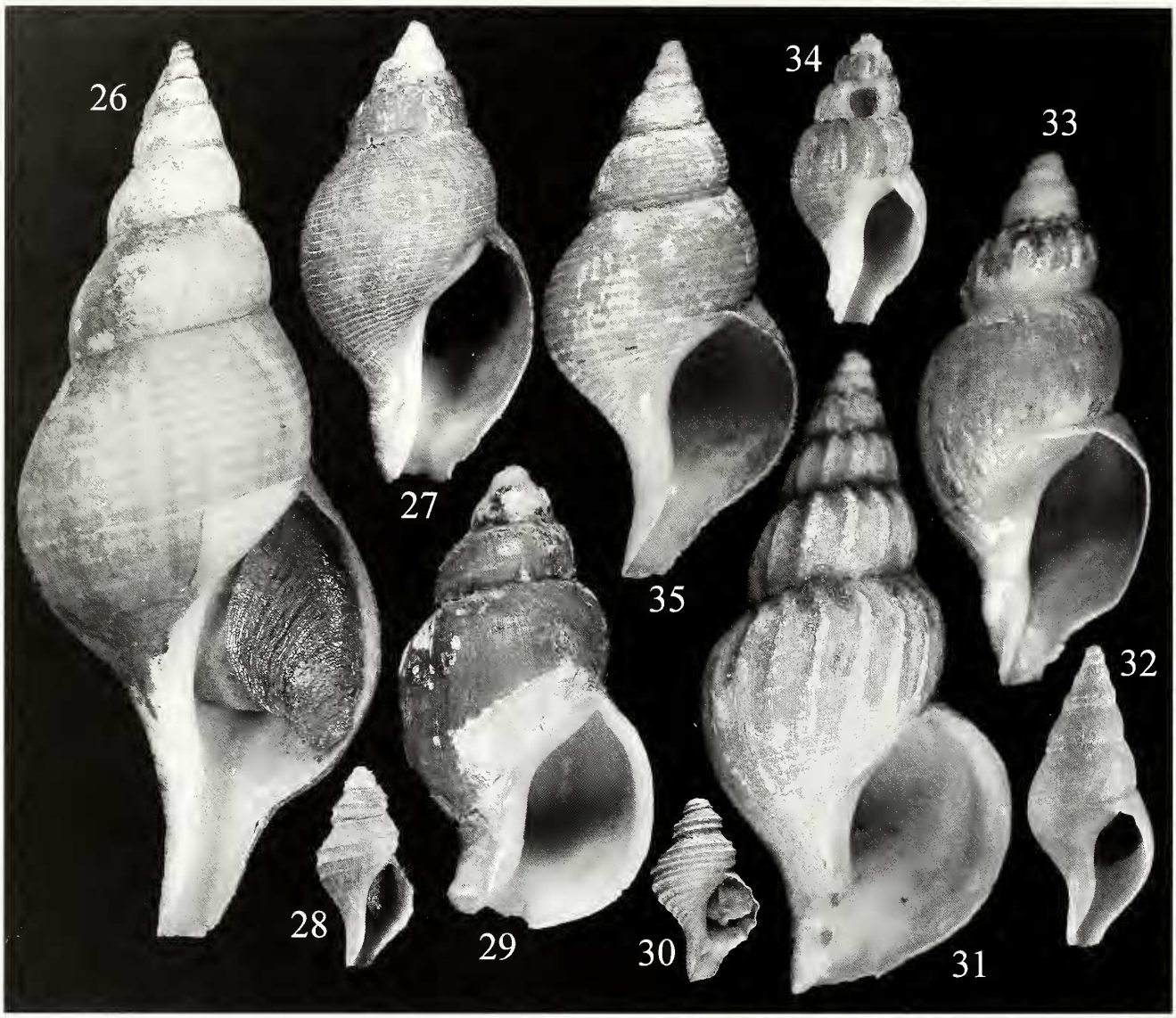
Genus Composition: We include the following species in *Retifusus*, although some others may belong to this group as well:

Retifusus jessoensis (Sehrenek, 1863) [= *Fusus (Sipho?) manchurieus* E. A. Smith, 1875; *Chrysodomus brunneus* Dall, 1877; *Molnia okhotskana* Tiba, 1981 – synonymy based on examination of the type specimens and anatomical studies .]
Retifusus frielei (Dall, 1891)
Retifusus virens (Dall, 1877)
Retifusus yamamii (Yokoyama, 1926)
Retifusus laticingulatus Golikov et Gulbin, 1977
Retifusus roseus (Dall, 1877) [= *Retifusus semiplieatus* Golikov *in* Golikov and Scarlato, 1985; *Plicifusus parvus* Tiba, 1980; *Plieifusus saginatus* Tiba, 1980 – synonymy based on examination of the type specimens and anatomical studies].
Retifusus similis (Golikov et Gulbin, 1977)
Retifusus attenuatus (Golikov et Gulbin, 1977)
Retifusus iturupus (Golikov et Sirenko, 1998)

Retifusus differs from *Plicifusus* in radular morphology; from *Molnia* in the form of its opereulum, the presence of axial sculpture and in radular morphology; from *Colus*, *Aulaeofusus*, and *Latisipho* in axial sculpture and radular morphology.

Clade 5 includes representatives of *Aulaeofusus* that are rather uniform conchologieally and morphologieally.

Figures 18–24. Anatomy. **18.** Transverse section of the proboscis wall of *Aulaeofusus hereudeeni*. **19, 20.** Transverse section of the proboscis wall of *Aulaeofusus brevicauda*. **21.** Salivary ducts of *A. brevicauda*. **22.** Transverse section of the proboscis wall of *Retifusus jessoensis*. **23.** Salivary duct of *R. jessoensis*. **24.** Transverse section of the proboscis wall of *Plicifusus lastarius*. Abbreviations: **aoe,** anterior esophagus; **cm,** circular muscles; **cnt,** connective tissue; **crt,** odontophoral cartilage; **ep,** epithelium; **lm,** longitudinal muscles; **n,** nerves; **r,** radula; **sd,** salivary duct.



Figures 26–35. Shells. **26.** *Colus islandicus*. **27.** *Latisipho hallii*. **28.** *Pararetifusus tenuis*. **29.** *Latisipho hypolispus*. **30.** *Pararetifusus kantori*. **31.** *Plicifusus kroeyeri*. **32.** *Retifusus attenuatus*. **33.** *Plicifusus rhyssus*. **34.** *Retifusus jessoensis*. **35.** *Aulacofusus brevicauda*.

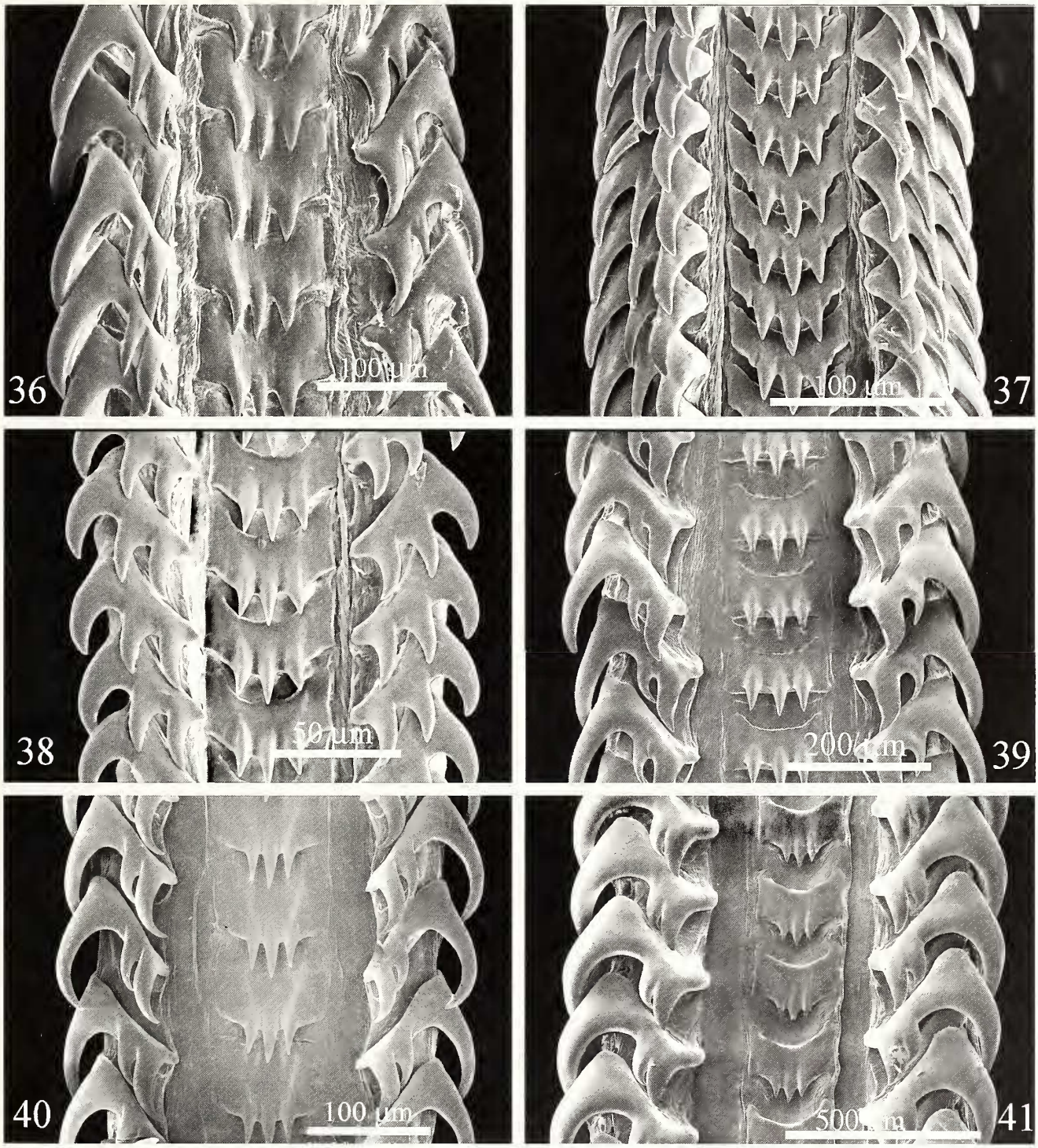
Aulacofusus Dall, 1918

Aulacofusus Dall, 1918: 217.

Type Species: *Fusus spitzbergensis* Reeve, 1855 (by original designation).

Diagnosis: The group is characterized by an elongated, medium-sized fusiform shell sculptured with wide spiral cords (from 6 to 16 cords on the penultimate whorl) (Figure 35). The axial sculpture is represented only by incremental growth lines. The radula structure is in general the same as in *Plicifusus* (Figure 39). The salivary ducts are thick-walled, with an additional external layer of longitudinal muscles (Figure 21, **lm**). The stomach is large, as compared to the proboscis, and narrow, with a very long posterior mixing area (Figure 16, **pma**).

Remarks: The taxon was proposed as "group of species, typified by *Fusus spitzbergensis* Reeve that has a special aspect due to the short canal and the prominence of the spiral ribs..." Thus, the rank of the taxon was not specified, but it is obvious, from the context of the description, that Dall (1918) considered it even lower than that of a section of the genus *Colus*. Later, Dall (1921) treated it as subgenus of *Colus*, a view that has been followed by most recent authors (e.g., Higo et al., 1999), but not by some Russian researchers (e.g., Golikov and Gulbin, 1977; Kantor and Sysoev, 2005, 2006).



Figures 36–41. Radulae. **36.** *Plicifusus kroeyeri*. **37.** *Retifusus jessoensis*. **38.** *Pararetifusus kantori*. **39.** *Aulacofusus brevicauda*. **40.** *Latisipho hypolispus*. **41.** *Colus islandicus*.

Species of *Aulacofusus* have a considerable conchological similarity to species attributed to the genus *Colus*, particularly in the shape and sculpture of the shell (Figures 26, 35). Some anatomical characters, such as the extremely long, coiled proboscis typical of *Aulacofusus* (Figure 14), are also present in some species of *Colus*. Nevertheless, the presence of several autapomorphies of *Aulacofusus*, including stomach structure that is

Table 1. Character coding (see Appendix 1).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Volutopsius norvegiens	0	0	1	0	1	0	2	0	0	?	1	1	2	1	?	1	?	0	0	1	0	0	2	2	0	1	0	1	1	2	2	1	0	0
Plicifusus kroeyeri	0	1	0	0	0	0	0	0	0	0	0	0	1	0	?	?	?	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0
Plicifusus plicatus	0	1	0	0	0	0	0	0	0	?	0	0	0	0	?	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Plicifusus croceus	0	1	0	0	0	0	0	0	0	?	0	0	0	0	?	0	?	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Plicifusus scissuratus	0	1	0	0	0	0	0	0	0	?	0	0	0	0	?	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Plicifusus elacodes	0	1	0	1	0	0	0	0	0	?	0	0	0	0	?	0	?	0	0	1	0	0	2	1	2	0	0	0	0	0	1	1	0	0
Plicifusus oceanodromae	0	1	1	0	0	?	?	0	?	0	0	0	0	0	?	0	?	0	0	1	2	1	1	0	1	0	0	0	0	0	1	0	0	0
Plicifusus hastarius	0	1	0	0	0	?	?	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1	0	0
Plicifusus bambusus	0	1	1	0	0	?	?	0	?	0	0	0	0	0	?	0	?	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Plicifusus olivaceus	0	1	0	0	0	0	0	0	0	?	0	0	1	0	?	0	?	0	0	0	0	1	1	1	1	1	0	1	1	0	1	0	0	0
Plicifusus obtusatus	0	0	1	0	0	0	0	0	0	?	0	0	0	0	?	0	?	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0
Plicifusus torquatus	0	0	0	0	0	?	?	0	0	?	0	0	0	0	?	0	?	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0
Plicifusus rhyssus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0
Colus islandicus	0	0	0	0	0	1	2	0	1	?	0	0	0	0	?	0	?	0	1	1	?	?	2	2	0	0	0	0	0	0	1	0	0	0
Colus kujianus	0	?	?	?	?	0	0	0	0	?	0	0	1	0	?	0	?	0	1	1	0	1	2	2	0	0	0	0	0	0	1	0	0	0
Colus minor	0	0	?	?	?	0	0	0	0	?	0	0	0	0	?	0	?	0	1	0	?	?	2	2	0	0	0	0	0	0	1	0	0	0
Colus gracilis	0	0	0	0	1	1	0	0	1	?	1	0	2	0	?	1	?	0	1	0	2	0	2	2	0	0	0	0	0	0	1	0	0	0
Colus jeffreysianus	0	0	0	0	1	?	?	0	?	?	1	0	2	0	?	1	?	0	1	0	2	0	2	2	0	0	0	0	0	0	1	0	0	0
Pararetifusus tenuis	1	0	1	1	1	?	?	0	?	1	0	0	3	0	?	0	?	0	1	0	0	1	2	2	2	0	1	1	1	0	0	0	1	0
Pararetifusus kantori	1	0	1	1	0	2	2	0	0	0	0	0	3	0	?	0	?	0	1	0	?	?	2	2	2	0	2	1	1	0	0	1	1	0
Pararetifusus kosugei	0	0	1	1	0	?	?	0	?	1	0	0	0	1	?	0	?	1	1	0	0	0	2	2	2	0	1	1	1	0	0	0	1	0
Retifusus virens	2	0	0	1	0	?	?	0	?	1	0	0	0	0	?	0	?	0	1	1	0	1	0	1	1	1	0	1	1	1	2	0	1	1
Retifusus laticingulatus	2	0	1	1	1	?	?	0	?	1	0	0	0	0	?	0	?	0	0	1	?	?	0	1	1	0	0	1	1	0	0	0	1	1
Retifusus similis	2	0	1	1	0	?	?	0	?	?	0	0	0	0	?	1	?	0	1	1	0	1	0	2	1	0	0	0	0	0	0	0	1	0
Retifusus attenuatus	2	0	1	1	0	1	?	0	?	?	0	0	0	0	?	1	?	0	1	1	0	0	2	2	1	0	0	1	1	0	0	0	1	0
Retifusus yanamii	0	0	1	1	0	1	0	0	0	0	0	0	0	0	?	0	?	0	1	0	0	0	0	1	1	1	0	1	1	1	2	0	1	1
Retifusus jessoensis	2	1	1	1	0	1	0	0	0	?	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	1	1	2	0	1	1
Retifusus frielei	1	1	1	1	0	1	0	0	0	?	0	0	1	0	?	0	?	0	1	0	0	0	0	1	1	0	0	1	0	1	2	0	0	1
Retifusus iturupus	0	0	1	1	0	1	?	0	0	?	0	0	0	0	?	0	?	0	0	0	?	?	0	1	1	0	0	1	1	0	0	0	1	0
Retifusus roseus	2	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0
Aulaeofusus brevicauda	0	0	0	1	0	?	?	0	?	1	1	1	2	1	0	1	1	0	1	1	1	0	2	2	1	0	0	0	0	0	1	0	0	0
Aulaeofusus herendeeni	0	0	0	1	0	2	2	0	0	?	1	1	2	1	?	0	1	0	1	1	1	0	2	2	1	0	0	0	0	0	1	0	0	0
Aulaeofusus ombronius	0	1	0	1	0	?	?	0	?	0	1	1	2	1	?	0	1	0	1	1	1	0	2	2	2	0	0	0	0	0	1	0	0	0
Aulaeofusus periscelidus	0	0	0	1	0	?	?	0	0	0	1	1	2	1	?	1	1	0	1	0	1	0	2	2	2	0	3	0	0	0	1	0	0	0
Latisipho hypolispus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	2	2	2	0	1	1	1	0	1	1	0	0
Latisipho hallii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	2	0	0	0	1	1	0	1	1	0	0
Aneistrolepis okhotensis	0	0	1	0	1	0	2	0	0	?	1	1	2	1	0	1	?	0	0	1	0	0	2	2	0	1	1	1	1	2	2	1	0	0
Neptunea antiqua	0	1	0	0	1	2	2	1	0	?	0	0	0	0	?	1	?	0	0	1	0	1	2	2	0	1	0	1	1	0	0	1	1	0
Neptunea jagudinae	0	0	1	1	1	2	2	1	0	?	0	0	0	0	?	1	?	0	0	2	?	?	2	2	0	1	0	1	1	0	0	0	0	0
Neptunea gulbini	0	0	0	0	0	0	0	1	0	?	0	0	0	0	?	1	?	0	0	2	0	1	2	2	0	1	0	1	1	0	0	0	0	0

unique in the entire subfamily Colinae, and the histological structure of the wall of the salivary ducts, lead us to treat it as a separate genus.

Genus Composition: Many species has been attributed to this group at various times. We include the following examined species in the subgenus:

Aulaeofusus brevicauda (Deshayes, 1832) (=*Tritonium schantarieum* Middendorff, 1849; *Neptunea (Sipho) terebralis* Gould, 1860)

Aulaeofusus herendeeni (Dall, 1899) (=*Colus (Aulacofusus) nobilis* Dall, 1919)

Aulacofusus ombronius (Dall, 1919)

Aulaeofusus periscelidus (Dall, 1891)

Clade 6 is the most basal elade in our study, and is supported in only 53% of the trees. It includes three speeies of the genus *Neptunea* Röding, 1798: *Neptunea antiqua* (Linnaeus, 1758) (type speeies of the genus by subsequent designation of Sandberger, 1861), *N. jagudinae* Goryachev and Kantor, 1983, and *N. gulbini* Goryaehev and Kantor, 1983. The genus was ineluded in the analysis based on published data (Goryaehev and Kantor, 1983) and its detailed description is beyond the scope of the current paper. Nevertheless, our analyses suggest that the genus in its conventional sense may be paraphyletie.

Both known species previously referred to *Latisipho* (Kosyan, 2006b) (Figures 27, 29), do not emerge as a

monophyletic group in our study, and their taxonomic position should be reconsidered.

Our study indicates that the anatomical characteristics are important and suitable for differentiating among the genera of Colinae and Buccinidae. Despite the absence, in many cases, of autapomorphies, many closely related genera may be diagnosed by combinations of characters through the use of phylogenetic techniques.

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APPENDIX 1. List of characters and character states.

Cephalopodium

1. Operculum: 0 — with terminal nucleus (Figure 1), 1 — with spiral nucleus (Figure 4), 2 — with terminal nucleus displaced to the left.

Mantle

2. Mantle: 0 — square, 1 — length exceeds width.
3. Osphradium: 0 — symmetrical, 1 — asymmetrical.
4. Osphradium: 0 — short (< ½ of mantle length), 1 — long (> ½ of mantle length).
5. Ctenidium: 0 — lamellae of ctenidium wider than lamellae of osphradium, 1 — lamellae of ctenidium of the same width as lamellae of osphradium.

Reproductive System

6. Penis: 0 — with large seminal papilla (Figures 6, 8, 9), 1 — with small papilla (Figure 10), 2 — without papilla (Figure 5).
7. Seminal papilla: 0 — cone-shaped, encircled by fold of skin (Figures 6, 8, 9), 1 — claw-like, 2 — absent.
8. Male genital opening: 0 — not surrounded by tiny papillae, 1 — surrounded by multiple tiny papillae.
9. Vas deferens: 0 — thin, convoluted, not protruding into body haemocoel, 1 — thick, located in body haemocoel.

10. Capsule gland: 0 — with ventrally folded vagina, 1 — with terminal vagina.

Digestive System

11. Proboscis: 0 — straight (Figures 12–13, pr), 1 — folded within rhynchocoel (Figure 14, pr).
12. Rhynchodeum: 0 — thick-walled, everting, 1 — thin-walled, non-everting.
13. Relative length of buccal mass: 0 — equal in length to contracted proboscis, 1 — half the length of the contracted proboscis, 2 — less than half the length of the contracted proboscis, 3 — longer than the contracted proboscis.
14. Proboscis retractors: 0 — running along rhynchodeum and attached to roof and lateral walls of body haemocoel (Figure 12–13, prr), 1 — short, situated at the base of the proboscis and attached to the bottom of body haemocoel (Figure 14, prr).
15. Sequence of layers in the proboscis wall [outer to inner edges]: 0 — epithelium, circular muscles, longitudinal muscles, circular muscles, longitudinal muscles (Figure 19), 1 — epithelium, longitudinal muscles, circular muscles, longitudinal muscles, circular muscles (if present) (Figure 24).
16. Salivary glands: 0 — small and rounded (< 1/3 of proboscis length) (Figure 12), 1 — long, bean-shaped (> 2/3 of proboscis length) (Figures 13, 14).
17. Salivary ducts: 0 — without additional longitudinal muscle layer in the wall (Figures 22, 23), 1 — with external layer of longitudinal muscles in the wall (Figures 20, 21).
18. Salivary ducts: 0 — without salivary sacs (Figures 13, 14), 1 — with salivary sacs (Figure 15).
19. Salivary ducts: 0 — thin, convoluted (Figure 13), 1 — thick, straight (Figures 14, 15).
20. Gland of Leiblein: 0 — well developed, 1 — thin, poorly developed, 2 — absent.
21. Stomach: 0 — with small posterior mixing area (Figure 17), 1 — with very long posterior mixing area (Figure 16), 2 — without posterior mixing area.
22. Stomach: 0 — large (>1/3 whorl), 1 — small (<1/3 whorl).

Shell

23. Axial ribs: 0 — < 14 axial ribs on last whorl, 1 — > 14 ribs on last whorl, 2 — axial ribs absent.
24. Axial ribs: 0 — s-shaped, 1 — straight, 2 — absent.
25. Spiral sculpture: 0 — numerous cords present (> 20 on penultimate whorl), 1 — few cords present (< 20 on penultimate whorl), 2 — cords absent.
26. Microscopic spiral threads: 0 — present, 1 — absent.
27. Spiral cords: 0 — absent, 1 — present, low, acute distally, 2 — present, rounded distally, 3 — present, flattened.
28. Ratio, body whorl height / shell height: 0 — <0.7; 1 — >0.71.
29. Ratio, aperture length / shell length: 0 — <0.5; 1 — >0.51.

Radula

30. Central tooth: 0 — with 3 cusps (Figures 36, 38–41), 1 — with multiple cusps, posterior tooth edge rounded (Figure 37), 2 — with multiple cusps, posterior tooth edge nearly straight.
31. Central tooth: 0 — with 3 cusps, all of equal size, 1 — with 3 cusps, medial cusp differing in size from the marginal cusps, 2 — with more or fewer than 3 cusps.
32. Lateral teeth: 0 — with 3 cusps, 1 — with more or fewer than 3 cusps.
33. Lateral teeth: 0 — medial cusps smallest, 1 — all cusps equal in length.
34. Cusps of the central tooth: 0 — do not overlap tooth of following row; 1 — overlap tooth of following row.